SPAWNING HABITAT CHARACTERISTICS OF PACIFIC HERRING (*CLUPEA PALLASII*) IN PRINCE WILLIAM SOUND, ALASKA

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Abstract

Spawning habitats of Pacific herring in Prince William Sound, Alaska were analyzed to determine the importance of habitat features including vegetation type, percent vegetative cover, substrate type, water depth, and shoreline slope in the importance of herring spawning ground selection. Sidescan sonar data were used to compare bottom habitat characteristics of herring spawning areas vs. non-spawn areas. No significant differences in vegetation or substrate type were detected between areas where herring do and do not spawn. Generalized linear models and analysis of variance models were constructed to predict the probability of herring spawn and estimate egg densities given habitat information collected by the Alaska Department of Fish and Game during herring egg deposition surveys. Habitat characteristics explained 31% of the deviance in spawn presence and absence and 28% of the variability in egg densities. Vegetation type was the most important variable in determining the presence of spawn and vegetative percent cover was the most important variable in determining the intensity of herring spawn. Herring spawned most often on brown and red filamentous algae and red foliose algae. Egg densities increased with increasing percent vegetative cover. Spawning occurred most frequently in the shallow subtidal zone from 0 – 4 m.

Table of Contents

List of Figures

List of Tables

Table 5. Results from the multi-way ANOVA of herring egg density given the following predictor variables (vegetation type, percent vegetative cover, substrate type, depth, slope, and year) and an interaction term for vegetation and substrate.

List of Appendices

Appendix

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Introduction*

Pacific herring (*Clupea pallasii* Valenciennes, 1847) are an important forage fish and support valuable fisheries over their entire range from southern California to the Bering Sea (Haegele and Schweigert 1985a). Pacific herring provide the major food base for many marine birds, mammals, and fish and are preyed upon throughout all stages of their life cycle. Herring eggs in the intertidal zone are heavily preyed upon, primarily by marine birds (Outram and Humphreys 1974). Other predators of herring eggs include sturgeon, smelt, surfperches, and crabs (Lassuy 1989). Herring larvae are consumed by pelagic invertebrates and juvenile salmonids. While inshore, adult herring are susceptible to predation by salmon, seals, sea lions, killer whales, dogfish, and birds (Hourston and Haegele 1980). When feeding offshore, herring are preyed upon by sablefish, dogfish, Pacific cod, and salmon (Lassuy 1989). In addition to being an important forage fish, Pacific herring support valuable commercial, personal-use, and culturally important fisheries. Pacific herring have been harvested for many centuries by Native Americans for use as a fresh or salted food source, for trade or for bait (Hourston and Haegele 1980). Since the early 1900s, herring have supported numerous highly productive commercial fisheries.

Prince William Sound (PWS) is a small semi-enclosed sea separated from the Gulf of Alaska by a series of mountainous islands where there are important herring fisheries (Figure 1). Currently, herring are fished for roe, spawn-on-kelp, human consumption and bait. The

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average commercial harvest of Pacific herring in PWS was valued at $5.5 million from the late 1970s to the early 1990s. During this time period catch values ranged from a high of $12.2 million in 1992 to a low of $187,000 in 1996 (Sharp et al. 2000). Prior to 1993, the herring population in PWS was at a high level of abundance (~ 90,000 mt) and increasing (Marty et al. 1999). In 1993, the PWS herring population crashed apparently due to viral hemorrhagic septicemia virus (VHSV) (Marty et al. 1999). As a result, herring fisheries were reduced in 1993 and closed from 1994 to 1996. Herring fisheries resumed in PWS in 1997 and 1998 and closed again in 1999 due to the occurrence of VHSV and low spawning stock abundances (Norcross and Brown 2001). Herring fisheries in PWS have not reopened.

Spawning grounds of Pacific herring are typically in sheltered inlets, sounds, bays, and estuaries rather than along open coastlines (Haegele and Schweigert 1985a). Pacific herring spawn demersally in intertidal or shallow subtidal waters (Hay 1985) to a maximum depth of 20 m (Wespestad and Barton 1987). Spawning ground locations are generally consistent from year to year (Haegele and Schweigert 1985a, Hay and Outram 1981) although abrupt shifts in spawn location have been known to occur (Robert Larson, personal communication, Alaska Department of Fish and Game P.O. Box 667 Petersburg, Alaska 99833). Reasons for ephemeral spawning grounds are unknown, though it has been hypothesized that Pacific herring expand their spawning distribution in years with large population sizes and contract their spawning grounds when the population decreases (Hay and Kronlund 1987). The location of Pacific herring spawning grounds makes them susceptible to impacts from coastal development and runoff (Funk 2000). Most herring spawning habitat in Alaska is

undeveloped and has not been degraded by human activities (Funk 2000); however, managers often lack adequate information to make informed decisions on issues that could potentially affect herring spawning habitat.

Many studies have considered Pacific herring spawning; however, very few have focused on the importance of specific habitat types for spawning bed selection. Research on Pacific herring spawning grounds in Alaska is especially lacking compared to other areas. Recently, spawning bed characteristics were described for Pacific herring in Japan (Hoshikawa et al. 2001) and Baltic herring (*Clupea harengus membras* L.) in SW Finland (Kääriä et al. 1997). In British Columbia, fishery-monitoring data were used to (1) construct a model for estimating Pacific herring spawn density (Schweigert and Fournier 1982), (2) describe the distribution and characteristics of herring spawning (Hay and Kronlund 1987; Haegele and Schweigert 1985a; Barton and Wespestad 1980), and (3) determine the distribution of Pacific herring eggs by depth and vegetation type (Haegele et al. 1981). Data compiled on herring spawn distributions along the coast of British Columbia show how these spawning areas changed from 1928 through 1999 (Hay et al. 2001). Over 5,200 km of British Columbia's coastline were ranked and classified as herring spawning habitat (Hay et al. 2001). Approximately 12% of the British Columbia coastline is used by herring for spawning, although much less of the coast is used for repetitive spawning over a number of years. In recent years, interest and concern about the protection of herring spawning grounds in British Columbia have increased by industry, the government and the public. It is believed that

areas of repeat spawnings over time deserve the most protection from environmental degradation (Hay et al. 2001).

Other research related to Pacific herring spawning has been conducted on egg loss rates and the habitat factors that control eggs loss in PWS and British Columbia (Rooper et al. 1999, Schweigert and Haegele 2001). In Alaska, average depth of egg deposition, cumulative time of egg exposure to air, location and exposure to waves, substrate type, vegetation type, and bird abundance are all important factors in determining the rate of egg loss over time (Rooper et al. 1999). Although important in Alaska, predation by birds, depth of egg deposition, and exposure to waves do not to explain egg loss in British Columbia (Schweigert and Haegele 2001). In British Columbia, the average egg loss rate is estimated to be 0.10 d^{-1} and egg loss is estimated by multiplying the time lapsed from spawn to the survey.

The density of egg patches for demersally spawning clupeoids is regulated by spawning behavior of the parents and by the availability of a suitable habitat (Blaxter and Hunter 1982). Pacific herring egg deposition varies in density from thinly scatter layers to more than 20 layers (Haegele and Schweigert 1985a). Four factors that contribute to suitable herring spawning habitat are shoreline slope, depth, vegetation and substrate (Barton and Wespestad 1980, Haegele and Schweigert 1985a, Hay 1985). Therefore, herring spawning location and intensity is a function of the habitat characteristics of an area to some extent.

Most herring fisheries take place during the spawning event when the fish are congregated in shallow nearshore areas. The Alaska Department of Fish and Game (ADF&G) has monitored Pacific herring spawning distributions in PWS with aerial surveys since 1973 and with dive surveys since 1983 (Sharp et al. 2000). Data collected from these surveys allow ADF&G to estimate herring spawning stock biomass to set harvest quotas and seasons for the fishery. Aerial surveys are conducted to determine the major areas receiving spawn and to estimate total miles of spawn. Dive surveys are conducted to quantify the amount of spawn along randomly selected transects. Egg deposition estimates from dive surveys are extrapolated to miles of spawn; information on the age distribution and sex ratio of the stock, mean weight at age, fecundity, and estimates of egg loss are incorporated to estimate the spawning stock biomass in a region (Willette et al. 1998). Auxiliary information collected during dive surveys includes water depth and the type of vegetation and/or substrate to which the eggs are attached. Though a large egg deposition database exists, data have not been analyzed to link herring spawn distribution and abundance with other variables collected during the surveys.

Vegetation type, percent vegetative cover, substrate type, water depth, shoreline slope and exposure of Pacific herring spawning areas in PWS are analyzed in this study to determine the role of habitat in spawning ground selection. Three analyses on two spatial scales are preformed to detect differences in habitat where herring have and have not spawned historically. The coastline within PWS is highly irregular with numerous islands, inlets, bays and deep fjords (Norcross et al. 2001). The broad scale analysis compares herring spawn and

non-spawn areas on the level of entire bays or islands. The fine scale analyses compare habitat characteristics on the scale of sampling units within egg deposition survey transects for the presence and absence of spawn and for differences in egg densities.

Methods

Broad Scale

Habitat selectivity of spawning herring was inferred by comparing the habitat characteristics in areas where herring spawn to areas where herring do not spawn. The objective was to compare the substrate and vegetation compositions in areas where herring do and do not spawn to determine patterns of habitat selection for spawning.

Habitat data were obtained for areas where herring spawn and where herring are not known to spawn. ADF&G dive surveys only occurred in areas where herring have spawned. Survey years included in this study were 1988-1992, and 1994-1997. Dive survey transects provided a systematic estimation of egg density across the spatial distribution of eggs. Detailed methods for dive surveys (egg deposition transects) in PWS can be found in Becker and Biggs (1992). Sidescan sonar surveys conducted in selected areas of Prince William Sound in 1995-96 provided habitat assessment independent of herring spawning. As part of the Exxon Valdez Oil Spill Nearshore Vertebrate Predator (NVP) study, five locations in PWS were surveyed with sidescan sonar to determine the subtidal substrate composition (Holland-Bartels et al. 1998). The surveys coincidently covered 2 areas where herring have spawned and 3 areas where herring have not been known to spawn. The areas surveyed were

portions of Montague Island, Bay of Isles, Herring Bay, Jackpot Bay and Naked Island (Figure 1). According to annual herring spawn distributions from aerial surveys conducted by the ADF&G from 1973 to 1997, Montague and Naked Islands were areas where herring have consistently spawned and the Bay of Isles, Herring Bay and Jackpot Bay represented the non-spawn areas. The "spawn" areas surveyed by the sidescan sonar consisted of areas where dive surveys had taken place.

Sidescan sonar surveys and dive surveys classified habitat differently. Thus, it was necessary to test the feasibility of generating habitat categories that could be matched by the two survey procedures. A principal difference was that the dive survey data had separate vegetation and substrate categories whereas the sidescan data had one category where substrate type was noted only if conspicuous vegetation was absent. Vegetation types could be assigned to the substrate types classified by the sidescan sonar (and vice versa) if it could be shown that vegetation type was dependent on substrate type and that the two were functionally related (Dillon and Goldstein 1984). Dive survey substrate types were aggregated into groups based on grain size to match the sidescan sonar categories. Using all of the dive survey transects, a contingency table of vegetation (rows) and substrate (columns) was generated and a chi-square test of independence was applied to test the null hypothesis of no relationship between vegetation and substrate frequencies. A Goodman-Kruskal measure of proportional reduction in error (PRE) was calculated to determine if vegetation and substrate were functionally related (Dillon and Goldstein 1984).

The dive survey database included geographic coordinates for the origin of the dive transect. During the surveys, observations were conducted systematically every 5 m along the transect. Station points were generated from the dive survey transect coordinates to spatially represent these observations. Transect points were plotted on a NOAA nautical chart in ArcView (Environmental Systems Research Institute Version 3.2). The azimuth of each transect was determined visually so that each transect would intersect the shoreline at a 90° angle. An ArcView script was used to generate points at a specified distance and azimuth from the origin point (Jenness 2001)(Figure 2). A relational join was used to link the habitat attribute information to the station points.

Sidescan sonar data were tested to determine whether they could be used as a reasonable proxy for dive data in areas where herring have not been known to spawn; the two data sources were spatially compared for differences in their habitat attributes in areas of overlap. The sidescan sonar data were plotted in a GIS in the form of polygons. Each polygon contained an attribute describing the seafloor substrate type (Figure 3). The dive survey station points were overlaid on the sidescan sonar polygons. The dive survey stations represented $0.1m^2$ quadrats and the sidescan sonar polygons were sliced into 1 m wide polygons in the areas where the two surveys overlapped. The corresponding sidescan sonar substrate type was assigned to each dive station. A contingency table of sidescan sonar substrate versus dive survey substrate revealed that it was not possible to combine the dive survey and sidescan sonar data for comparisons at the individual transect scale. Therefore, comparisons of spawn and non-spawn areas were conducted on larger, area-wide (i.e. bay or island) scale using the areas surveyed by sidescan sonar.

Vegetation and substrate compositions in spawn areas were compared to non-spawn areas by calculating the proportion of each bottom type in each area. Wilcoxon rank sum tests (Conover 1980) were used to test the null hypothesis that the proportion of each substrate and vegetation type was the same between the spawn and non-spawn areas. This test was used because it does not assume that the observations come from normal distributions.

Fine Scale – Presence/Absence

The analysis in the preceding section examined habitat differences between spawn and non-spawn areas over several continuous kilometers of shoreline whereas this analysis compares habitats with spawn present and absent from systematic samples conducted every 5 m along a transect. This level of analysis required classifying vegetation types from the dive survey database into general categories based on taxa and physical appearance similar to the classifications presented in Haegele et al. (1981). Vegetation types were first grouped by phylum (Chlorophyta, green algae; Phaeophtya, brown algae, Rhodophyta, red algae; and Anthophyta, eelgrass) and then by blade structure (foliose or filamentous). Foliose brown algae were classified as large kelp (i.e., *Laminaria* sp., *Nereocystis* sp.) or *Fucus* sp. Thirty-five vegetation types were grouped into eight categories (Appendix A).

A generalized linear model (GLM) was fit to the egg presence/absence data to determine the probability of the occurrence of spawn as a function of habitat. Habitat features recorded during the dive surveys were vegetation type, substrate type, depth (m) and the estimated vegetative percent cover. Additional habitat variables calculated for this study were slope

and exposure. The slope of each station was calculated by dividing the change in depth by the change in distance from the previous station. The exposure, defined as exposed or protected, of each transect was determined by examining the location of each transect overlaid on a nautical chart in a GIS. Transects were classified as being exposed if they were located on a headland or protected if they were within an embayment according to Rooper et al. (1999).

Logistic regression was used to model the binary response of "spawn present" or "spawn absent" as a linear relationship of the habitat characteristics. By their nature, binary response data violate the assumptions of classical linear models, however, through a process of reparameterization, GLMs induce linearity and allow a nonconstant variance to be directly incorporated into the analysis (Chambers and Hastie 1992).

A GLM requires two functions, a "link" function that describes how the mean depends on the linear predictors and a variance function that captures how the variance of the response variable depends on the mean. The logistic regression model is defined by the *logit* link function, expressed as:

$$\eta = \log\left(\frac{\mu}{1-\mu}\right)$$

and the binomial variance function $V(\mu) = \mu(1-\mu)$ (Chambers and Hastie 1992). The dispersion parameter (σ^2) for the binomial variance function is taken to be 1. Usually the

variance in the data is greater than that predicted by the binomial model ($\sigma^2 > 1$) which is referred to as over-dispersion (McCullagh and Nelder 1983). The assumption of binomial variance was validated by estimating the dispersion parameter with quasi-likelihood (McCullagh and Nelder 1983, Chambers and Hastie 1992).

The Splus GLM function uses an iterative reweighted least squares algorithm (IRLS), to fit GLMs (Chambers and Hastie 1992). The IRLS produces maximum likelihood estimates of the model parameters (McCullagh and Nelder 1983). The sequence in which terms are added to GLMs is relevant. The importance of each independent variable may differ according to the order in which terms are added to the model. The order for adding terms to the model was determined by fitting the model with one independent variable at a time and comparing the fit to the null model. Terms were added to the model in order of their importance in explaining the null deviance. The initial model consisted of the saturated main-effects model:

$$logit(\mu) = \alpha + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4 + \beta_5 x_5 + \beta_6 x_6 + \beta_7 x_7$$

where the dependent variable was the probability of spawn and the independent variables were vegetation, percent vegetative cover, depth, substrate, slope, year and exposure. Insignificant factors were sequentially removed from the analysis. The initial model was compared to the final model with a chi-square test for independence to determine the effect of removing the insignificant terms. The estimated coefficients of the habitat variables were

compared with one another to determine the influence of each level of each factor on the probability of the presence of spawn.

Two interaction terms were added to the final main-effects model to examine the interaction effects between vegetation and depth and vegetation and substrate. The interaction model was compared with the main-effects model with a chi-square test for independence to determine the improvement in the fit with the inclusion of the interaction terms.

The independent variables were analyzed individually to assess general differences in the presence and absence of spawn. Each of the categorical independent variables was analyzed for differences in the proportion of the presence or absence of spawn among each of its levels. Proportions represented counts of the number of occurrences of spawn present or absent in each level of the factors. Proportions of presence/absence were calculated for each type of vegetation and substrate and for each year. Differences in slope, depth, and vegetative percent cover between stations with spawn and stations without spawn were tested with one-way ANOVA.

It was postulated that vegetation may be confounded by depth and/or substrate type and that percent vegetative cover may be confounded by vegetation type. Confounding among the predictor variables was evaluated in two ways. First, the order in which terms were added to the model was varied to determine the effect of adding depth and substrate to the model prior to vegetation type and adding vegetation type prior to percent vegetative cover. Because the importance of each term is assessed after the effects of the terms added previously, the

importance of vegetation would decrease by adding depth (or substrate) first if vegetation type was confounded by depth (or substrate). If vegetation were confounded by depth or substrate type the effect of these variables alone would be as important if not more important in predicting the probability of spawn than the type of vegetation alone. Confounding among the predictor variables was further investigated by examining the correlation matrix of the estimated coefficients from the main-effects GLM.

Fine Scale – Egg Density

The finest scale analysis in this series was to determine the relationship between herring egg densities and the covariates collected during the dive surveys. Only stations with spawn present were included in this portion of the analysis to determine the effect of habitat characteristics and year on varying egg densities. Egg densities within the dive survey database were corrected by the ADF&G to account for egg loss between spawn deposition and dive surveys (Willette et al. 1998).

The raw egg densities were not normally distributed and required transformation (Figure 4). Extreme observations were eliminated before transforming the data. Egg densities from 0 to 1,000 eggs\0.1m^2 and greater than 1,000,000 eggs\0.1m^2 were removed from the dataset. A $\log_{10}$ transformation was applied to the remaining egg densities to approximate normal. A total of 6,492 observations remained after removing the extreme egg densities. Of the original egg densities, 8,209 were in the 0-1,000 eggs\0.1m^2 range and 9 observations were greater than 10,000 eggs/0.1m^2. Exploratory analyses were used to examine the relationship between the $\log_{10}$ transformed egg densities and each of the predictor variables (vegetation,

substrate, vegetative percent cover, depth, slope, and year) to visualize fluctuations in median egg densities within the various categories.

The relationship between the transformed egg densities and the predictor variables was modeled using a multi-way factorial ANOVA with unequal cell numbers. Vegetation percent cover, slope and depth were treated as categorical variables in the analysis. Year was included as a variable to account for variability in egg densities resulting from interannual differences in the spawning stock biomass and age-structure, both of which affect the overall egg abundance.

In this case, the initial model was the full model containing interactions for vegetation and substrate and vegetation and depth. The initial full model resulted in a poor fit so a parsimonious model was sought that could account for a similar amount of variance with fewer degrees of freedom. Factors that were determined to be insignificant in the full model were removed. The design was unbalanced, thus the order in which the variables were added resulted in different outcomes. To determine the order with which to include terms, a model was fit for each of the main-effects to see the reduction in the residual sum of squares (RSS) for each term. This process was followed by fitting the interaction terms of vegetation and substrate and vegetation and depth to determine the reduction in RSS by including these interactions. Terms were added from highest to lowest to the final model according to the rank of their individual effect on the reduction of the residual variance.

Results

Broad Scale

There was a significant ($X^2 = 5491$, $p < 0.01$) relationship between vegetation and substrate frequencies. However, the estimated parameter of association (PRE) between vegetation and substrate was low (0.23) indicating that vegetation is of little value in predicting substrate. As a result, vegetation types were not predicted from the substrate types and the sidescan sonar habitat classifications were not converted into separate vegetation and substrate categories.

Forty-five dive survey transects comprised of 645 stations were found to overlap the sidescan sonar polygons. A comparison of the two data sources revealed that the dive survey data were much more heterogeneous than the sidescan sonar polygons. Of the transects compared, 96% of the sidescan sonar transects were comprised of one substrate type and only 8% of the dive survey transects were comprised of one substrate or vegetation type. On average, 3.3 dive survey substrate types aligned with one sidescan sonar substrate. The vegetation and substrate type along the dive transects frequently changed every 5 or 10 m as shown in Figure 5. Because of the stark contrast in resolution between the two data sources, it was not possible to compare areas where only sidescan data were available to areas where only dive survey data were available.

A total of 21.1 km^2 was surveyed with the sidescan sonar in the five areas. Gravel was the most commonly occurring bottom type in all of the areas except for Herring Bay where rock was the most abundant substrate type (Figure 6). Montague was the only area where large kelp was detected by the sidescan sonar and eelgrass was only found at Montague and Bay of Isles. Generally speaking, substrate types occurred in similar, relative frequencies in all 5 areas and showed no patterns between spawn and non-spawn areas (Figure 6). This was confirmed by the Wilcoxon rank-sum tests for differences between the substrate compositions in the spawn and non-spawn areas which were highly insignificant for rock ($n = 2$, $m = 3$, $W = 10$ and $p = 0.8$), gravel ($n = 2$, $m = 3$, $W = 8$ and $p = 0.8$), and silt ($n = 2$, $m = 3$, $W = 8$ and $p = 0.8$). The Wilcoxon test statistic could not be calculated for boulders, large kelp, or eelgrass due to the low frequency of occurrence of these substrate types and the small sample size.

Fine Scale – Presence/Absence

Comparisons of the relative frequency distributions of spawn present and absent showed which categories within each of the predictor variables had higher proportions of spawn present than absent. Vegetation types with a higher proportion of spawn present were brown and red filamentous and foliose algae, and eelgrass (Figure 7). Filamentous and foliose green algae had higher proportions of spawn absent. Proportions of spawn present and absent were approximately equal for large brown kelps and *Fucus* spp. Substrate types with a higher proportion of spawn present were boulders and rock (Figure 8). Spawn presence and absence were approximately equal on mud and sand substrate types. Gravel and cobble substrates

had less spawn present. Herring spawn was present on approximately half of the stations surveyed in most years, except for 1988, which had spawn on only 30% of the stations (Figure 9).

Results from one-way ANOVAs revealed that the mean values for slope and percent vegetative cover were significantly different ($n = 15,208$, $F = 155.9$ and 3277.8, $p < 0.001$) and that mean depths were not significantly different ($n = 15,208$, $F = 1.04$, $p = 0.31$) between stations with and without spawn. Stations containing spawn had higher percentages of vegetative cover and more gradual slopes than stations without spawn (Table 1).

The logistic regression was fit with 8,045 replicates with and 7,163 replicates without spawn. The quasi-likelihood estimated the dispersion parameter to be 0.998, which is approximately equal to the default binomial dispersion parameter of 1.0. Thus, it was determined that the assumption of binomial variance was not violated. All factors (vegetation type, vegetation percent cover, substrate type, depth, slope, and year) were found to be highly significant ($p<0.001$) in the full main-effects model except for exposure ($p=0.75$), which explained virtually none of the deviance between spawn presence and absence. The full main-effects model explained 31% of the total deviance (Table 2). Vegetation type accounted for most of the explained deviance (77%). Combined, vegetation and substrate type accounted for 84% of the explained deviance. After vegetation and substrate type, the parameters listed in order of their overall importance in the model were year (which accounted for 6% of the explained deviance), percent vegetative cover (5%), depth (3.5%) and slope (1.5%). There was no significant difference between the initial, main-effects model and the model containing only

the significant factors ($p = 0.185$). Therefore, exposure was excluded from all subsequent analyses.

The trends in the coefficients of the predictor variables generally matched the raw proportions of spawn presence/absence within each of the categories. The estimated coefficients show the strength and direction of the relationship between each category of the predictor variables and the probability of the presence of spawn. The strongest association was between "no vegetation" and the absence of spawn (Figure 10). The converse of this is a positive association between presence of vegetation and the presence of spawn. Vegetation types with the highest probability of spawn were brown filamentous algae followed by red foliose algae, eelgrass, and red filamentous algae. Green filamentous and foliose algae and large brown kelps were negatively associated with the presence of spawn. Vegetative cover greater than 40% had a positive association with the presence of spawn. In the substrate category, boulders and rock had a positive association with the probability of spawn whereas the smaller substrate types (cobble, gravel, sand, and mud) had a negative relationship with the probability of spawn. However, this category only accounted for 1.96% of the deviance. Depths in the shallow subtidal zone (0 – 4 m relative to mean low lower water) were positively associated with spawn; however, depth only accounted for 1.07% of the overall deviance. Slope accounted for <0.5% of the total deviance, though there was a trend of an increasingly positive association with the probability of spawn and a gradually upward sloping shoreline. There was a greater amount of herring spawn in 1989 through 1991 and in 1994.

The logistic regression including interaction effects between vegetation and substrate, and vegetation and depth performed only slightly better than the model without interaction terms. The interactions were statistically significant ($p<0.001$), however including these two terms required three times as many parameters as the main-effects model and only accounted for an additional 2.5% of the deviance between spawn presence and absence (Table 3). In other words, a 200% increase in the degrees of freedom resulted in less than a 10% improvement in the model fit.

Analyses to examine confounding among the predictor variables revealed that vegetation type was not confounded by depth or substrate and the type of vegetation did not confound percent vegetative cover. The order in which terms were added to the model revealed that the effect of vegetation type was more important than depth or substrate even when the effects of depth and substrate type were evaluated first. Additionally, the correlation matrix of the estimated coefficients revealed that there were no strong correlations among the predictor variables. Correlation coefficients ranged from a high of 0.377 to a low of -8.0×10^{-6} with a mean of 0.00.

Fine Scale – Egg Density

Boxplots of each of the independent variables and egg densities revealed subtle trends (Figure 11). Patterns for egg densities were similar to patterns in spawn presence and absence. Herring spawned in the highest densities on brown and red filamentous algae and red foliose algae. Within the vegetation category, median egg densities were lowest on green

filamentous algae and unvegetated quadrats. Boulder and rock had slightly higher median egg densities than the other substrate types. Within the depth category, the highest egg densities occur in the shallow subtidal zone, in the range from –2 to 2 m. Within the slope category, the lowest median egg densities occurred in places with a gradual slope, however, there is little variation in egg density with changing slope. The highest and lowest egg densities occurred in 1988 and 1995 respectively. The most apparent pattern revealed by the boxplots was egg densities increasing with percent vegetative cover.

All terms were significant in the initial analysis of variance model containing all of the main-effects and interaction terms for vegetation and substrate and vegetation and depth (Table 4). The initial model explained 28% of the variance. Vegetation percent cover, year, and vegetation type explained most of the variance (Table 4). Slope and depth accounted for a minimal amount of the explained variance in egg density (0.8% and 1.0% respectively).

The final model consisted of significant factors that explained most of the variance in egg density in the initial model. The retained factors were percent vegetative cover, year, vegetation type, substrate type, and an interaction term for vegetation and substrate. All terms were significant (Table 5). The main-effects explained more of the variation than the interaction terms over fewer degrees of freedom. The final model explained the same amount of variance (28%) as the full model over fewer degrees of freedom (42% less) (Table 5).

Fine Scale Presence/Absence vs. Egg Density

Habitat variables differed in their level of importance in determining the presence of eggs versus density of eggs. Vegetation type was much more important than any other variable in predicting spawn presence but ranked third in explaining variation in egg density. Percent vegetative cover explained most of the variation in egg density; greater amounts of spawn were found in areas of greater vegetative cover. Substrate type alone was more important in explaining the presence of spawn but the interaction between vegetation and substrate explained more variance in egg density.

There was disparity in the importance of depth as an explanatory variable between the presence of spawn and the egg density. Some depths appeared to be unsuitable for herring spawning but within the depths where herring did spawn, there were no trends in the densities of eggs.

Discussion

The sample size (15,208 observations from 846 transects) in this study of Pacific herring spawning bed characteristics is unprecedented. Previous studies have analyzed the importance of various physical and biological characteristics of herring spawning areas from diver observations with much smaller sample sizes (Haegele et al. 1981, Kääriä et al. 1997, and Hoshikawa et al. 2001). The distribution of Pacific herring eggs by depth and vegetation type in southern BC was investigated by surveying a total of 32 transects over 2 years (Haegele et al. 1981). Spawning bed selection of Pacific herring in relation to vegetation,

bottom character, and marcrobenthos was studied in northern Japan by diving on 27 transects consisting of a total of 337 stations (Hoshikawa et al. 2001). Spawning bed characteristics of Baltic herring were described based on diver observations from a total of 19 transects (Kääriä et al. 1997).

Herring appear to be selecting for certain habitat types for spawning in PWS. Herring select against areas without vegetation and showed preference within the type of vegetation on which they spawned. In studies conducted in BC, however, herring do not appear to favor one vegetation type over another, rather the type of vegetation upon which the eggs are laid is a function of the depth at which the eggs are deposited and the type of vegetation found in a given area (Haegele and Schweigert 1985a). Despite this contrast, the occurrence of spawn on various vegetation types in PWS is similar to a study in BC where red algae was the primary spawn substrate followed by eelgrass, *Fucus* sp. and large brown kelp (Haegele 1981). The presence of large brown kelp is negatively associated with the presence of herring spawning in PWS and Japan (Hoshikawa et al. 2001).

The same vegetation types did not affect spawn presence and egg density to the same degree. In PWS, spawn is deposited most often and in greatest densities on brown and red filamentous, and red foliose algae. Spawn is most likely to be present in areas with vegetation, yet egg densities were lower on green filamentous algae than they were in unvegetated areas. Green algae do not appear to be important vegetation types for herring spawn in British Columbia (Haegele and Schweigert 1985a); however, Baltic herring spawn

occurred most frequently on filamentous green algae in SW Finland (Kääriä et al. 1997). The frequencies with which vegetation types occur in the samples used in this study are provided in Appendix B. Large brown kelps and green algae were the most and least frequently occurring vegetation type in the samples. The low occurrence of green filamentous algae may explain the apparent low importance of this vegetation type in PWS. The occurrence of brown and red filamentous and red foliose algae is also fairly low (6%, 5%, and 3% respectively) yet these vegetation types have a large effect on the presence of herring spawn indicating that herring spawn on these vegetation types disproportionately than on the other vegetation types. The apparent preference for red and brown filamentous algae may be explained by the probability of hatching success on these vegetation types. Hatching success is generally reduced at greater egg densities; this is especially true if the eggs are deposited on flat surfaces where the interstitial spaces are small (Hourston et al. 1984). However, branched filamentous algae have greater amounts of interstitial space to facilitate the flow of water and circulate oxygen through the egg layers and hatching success at higher egg densities is greater on these types of algae (Hourston et al. 1984). Pacific herring appear to spawn less on large brown kelps that have a slimy mucus surface that can slough sheets of herring spawn during periods of wind or wave activity.

Egg density is more a function of depth than it is of vegetation type (Hagele and Schweigert 1985a) and vegetation types are confounded by depth (Rooper et al. 1999). Spawn is most commonly deposited in the shallow intertidal and shallow subtidal zones of PWS, similar to studies in other areas (Hoshikawa et al. 2001, Hagele et al. 1981, Hourston et al. 1984)

however, depth explains virtually none of the variability in egg density in PWS. This finding is surprising as depth is the primary factor affecting the rate of egg loss in PWS (Rooper et al. 1999) and Pacific herring egg density increases with increasing depth in BC (Haegele et al. 1981). In this analysis, neither depth nor the interaction between vegetation and depth are useful in explaining variability in egg densities.

The amount of vegetative cover is an important factor in determining the density of Pacific herring spawn (Hoshikawa et al. 2001). The heaviest egg deposition occurs where the vegetation is the densest (Haegele and Schweigert 1985a). Percent vegetative cover explains most of the variance in egg density in PWS.

Shoreline slope is an important factor in the distribution of spawn in BC (Haegele et al. 1981); but does not have a large effect on the presence of spawn in PWS. Shoreline slope is a significant factor between spawn presence and absence and in explaining variability in egg densities in PWS. Though statistically significant due to the large number of samples analyzed in this study, shoreline slope has such a small effect on the density of eggs and the presence/absence of spawn that it is not likely to be biologically meaningful. Additionally, it appears that the shoreline slopes in BC are much more gradual on average than the shoreline used by Pacific herring for spawning in PWS. The full range of slopes considered in BC from steep (4.5%) to gradual (1%) (Haegele et al. 1981) are contained within the gradual category in this study (0 – 10%). Shoreline slopes within the areas used by spawning herring in PWS were as steep as 140% (a rise in 7m over a 5m interval). Most spawn in PWS is on

"gradual" slopes from 0-10%. More spawn is contained near the shoreward edge on gradually sloping transects and near the deeper edge of spawn on steeper transects (Haegele et al.1981), which indicates that in BC and in PWS eggs may not adhere to the substrate or vegetation as well on steep transects as they do on gradual transects and thus eggs accumulate at the bottom of steep transects. Therefore, herring may be selecting for gradually sloping transects where eggs are less likely to be lost.

Other studies have shown the importance of bottom substrate in spawning bed selection among Pacific, Atlantic (*Clupea harengus harengus*), and Baltic herring. Atlantic herring in the North Sea choose sand and gravel as the preferred spawn substrate (Maravelias et al. 2000) whereas Baltic herring select hard bottom types (Kääriä et al. 1997). Laboratory observations of Pacific herring spawning behavior show that rigidity and texture are important components of suitable substrates; a suitable substrate is rigid, smooth and free of sediment (Stacey and Hourston 1982). Pacific herring in PWS appear to be selecting for boulders and rock and against gravel and cobble. The selection of spawn substrates in PWS is intuitive given the vegetation types preferred for spawning and the stability of the various substrate types for supporting the preferred vegetation. For example, kelps often occur on rocky shorelines whereas sea grasses are associated with muddy bottom types. Unstable substrate types such as loose cobbles provide marginal habitat for marine vegetation as they are easily detached by wave or current action (Waaland 1977). Vegetation types are dependent on the type of substrate to which they were attached, however, vegetation and

substrate do not appear to be completely confounded as the effect of substrate independent of the effect of vegetation is explaining some of the variance in the presence of spawn.

Overall, the linear model explains only 28% of the variation in egg densities and the logistic regression model explains only 33% of the total deviance between spawn presence and absence indicating that forces other than the physical habitat characteristics contribute to herring spawning ground selection. The data used in this analysis were all from herring spawning areas and within these areas herring selected for some habitat types and against others. The unexplained variability between the presence and absence of spawn may in part, be due to the sampling design used to collect the data used in this analysis. Because surveys are conducted where herring spawn has been detected as density of milt from aerial surveys, it is possible that the habitats being surveyed are only within the most suitable herring spawning grounds and that marginal habitats are not surveyed. Aerial surveys since 1978 show the distribution of herring spawn to be concentrated in the eastern, northern and Montague portions of PWS. Traditional knowledge indicates that herring spawned along the western coastline of PWS prior to the 1964 earthquake. Suitable herring spawning habitat in western PWS may have been altered by uplift that resulted from the earthquake (Brown et al. In Press). The data used in this analysis are opportunistic in that they are being used for a purpose outside of the purpose for which they were collected. As such, results should be interpreted with caution. An unbiased analysis of herring spawn and non-spawn habitat should incorporate surveys conducted in areas where herring are known to spawn, areas where herring have spawned in the past, and areas where herring have never spawned.

Additionally, a sampling unit larger than the $0.1m^2$ used in the ADF&G dive surveys is recommended to classify habitat characteristics between spawn present and spawn absent. However, the number of observations analyzed in this study reveals patterns that are extremely unlikely to be due to chance alone.

A large proportion of herring eggs are lost to predation, offshore transport, desiccation, and suffocation throughout their incubation period (Rooper et al. 1999). Natural selection dictates that herring stocks deposit their eggs in habitats where the number of viable eggs will be sufficient for the continued reproductive success of the stock. The reproductive strategy of herring may be to ensure evolutionary success only by the shear number of eggs that they lay or it may be a combination of the number of eggs combined with the selection of particular habitats. From this study one may conclude that within PWS herring spawning ground selection cannot be explained by the physical habitat variables alone. It appears that herring select habitat types where egg loss will be minimized by depositing greater densities of eggs on vegetation types that facilitate the maximum amount of interstitial circulation and depositing fewer layers of eggs on vegetation types where egg loss has been determined to be high at higher densities. Spawn was also deposited preferentially in shallow subtidal depths where egg loss is minimized (Rooper et al. 1999). However, within the areas where herring spawn, habitat use is highly variable.

The sidescan sonar did not detect fine scale habitat changes and could not be used as a proxy for the dive survey data in areas where herring have not spawned, as was the original intent.

The sidescan sonar data could not be translated into specific sediment classifications and habitat was not delineated as precisely as desired (Holland-Bartels et al. 1998), indicating that there may be finer scale differences between herring spawn and non-spawn areas that were not detected by the sidescan sonar. The sidescan could distinguish rock from sand and eelgrass from other vegetation types, but it could not distinguish vegetation on rocks, or rock from rock with cover such as low lying algae (Tom Dean, Coastal Resources Associates, Inc. 1185 Park Center Drive, Ste. A Vista, CA 92083, Personal Communication). The targeted depth range for the sidescan sonar was the 4-10 m depth contour, which would overlap the depths surveyed by divers in the egg deposition surveys (Holland-Bartels 1998). However, in general, the sidescan sonar was positioned farther offshore than the targeted range (Holland-Bartels 1998) and there was not as much overlap in the dive survey and sidescan sonar transects as I originally anticipated. Diver observations in this study were much more heterogeneous than the sidescan sonar classifications; however, other investigators have detected close associations between acoustic and visual classifications of seabed habitat (Anderson 2001). Acoustic surveys calibrated by visual classifications made from a submersible indicated that habitat varied at similar scales between the two surveys, though the acoustic habitat classifications were generally less variable than the visual classifications (Anderson 2001). Despite these slight differences, acoustic systems can realistically sample habitats at scales that are relevant to biological study (Anderson 2001).

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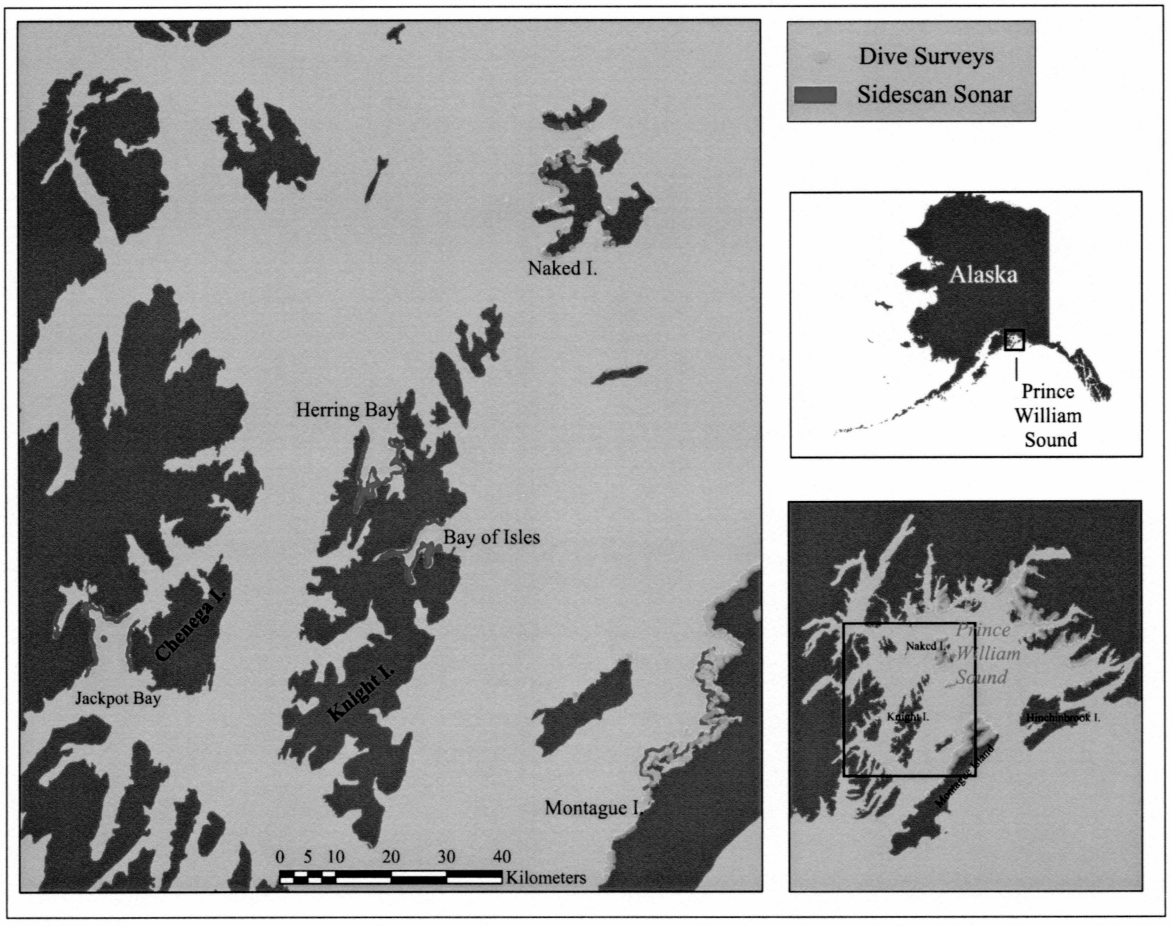


Figure 1. Prince William Sound, Alaska. This figure shows the locations surveyed by sidescan sonar during the Nearshore Vertebrate Predator (NVP) study (Holland-Bartels et al. 1998) (red lines) and the ADF&G dive survey transects (Becker and Biggs 1992) from 1988 – 1992 and 1994 – 1997 (yellow dots).

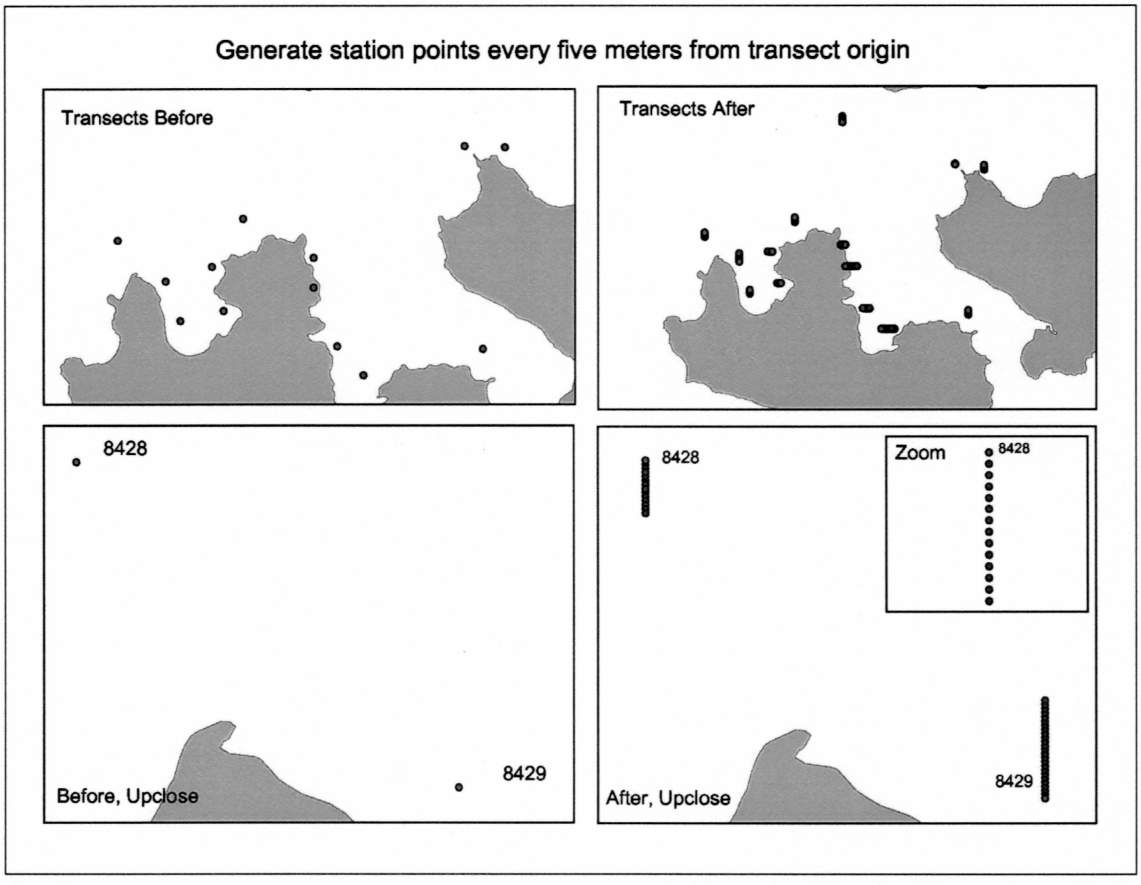


Figure 2. Example of ADF&G dive survey transects generated by plotting 5 m interval sample stations from the origin points that were provided in the herring egg deposition database.

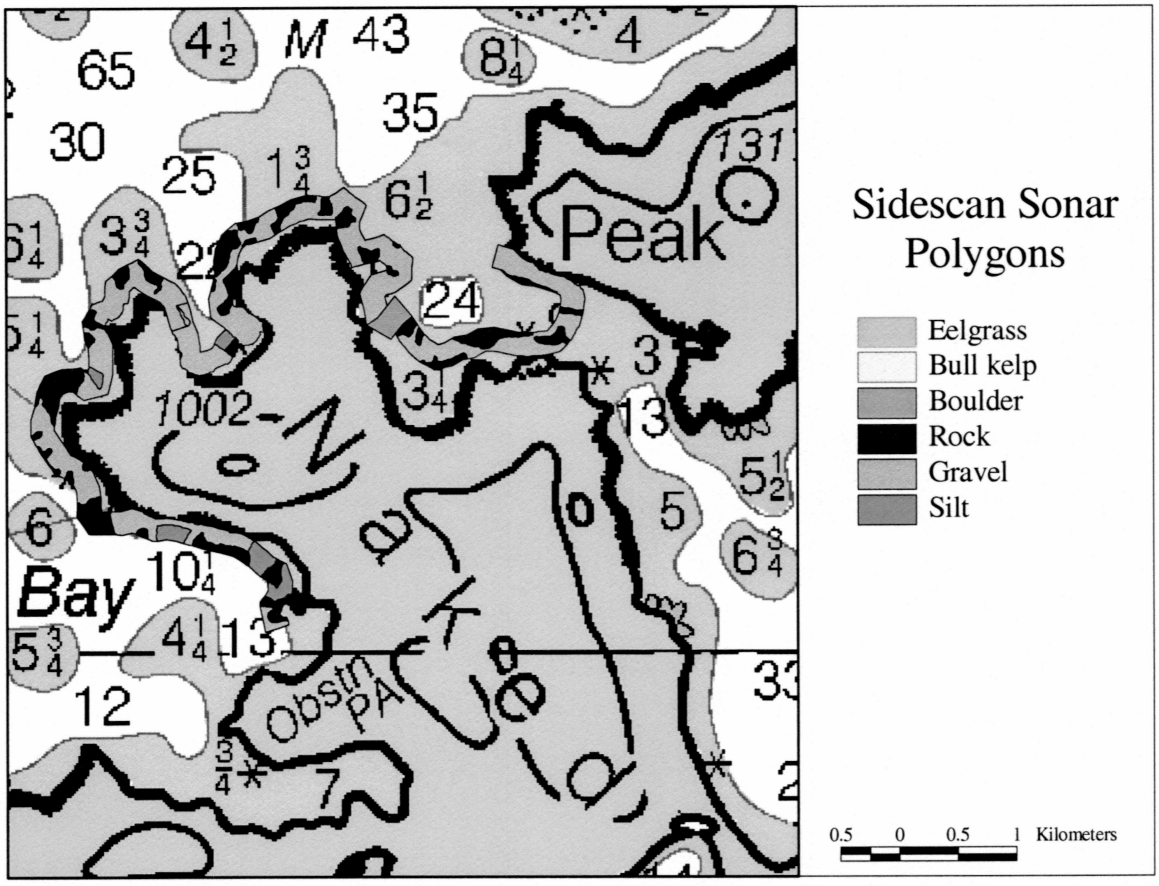


Figure 3. Example of sidescan sonar polygons (Holland-Bartels et al. 1998) used to compare bottom habitat types between herring spawn and non-spawn areas. This figure shows the bottom habitat types as classified by the sidescan sonar around Naked Island in Prince William Sound.

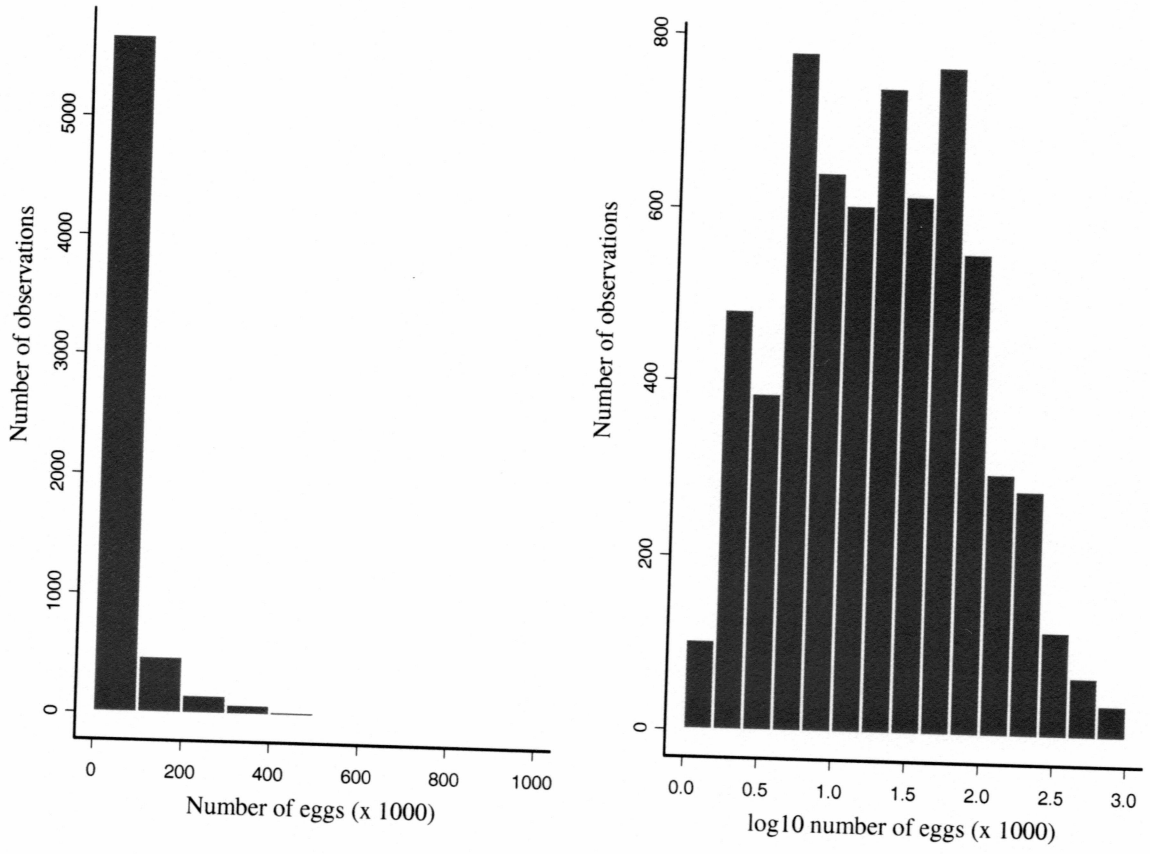


Figure 4. Distribution of herring egg densities from the ADF&G dive survey database before (left) and after (right) applying a $\log_{10}$ transformation.

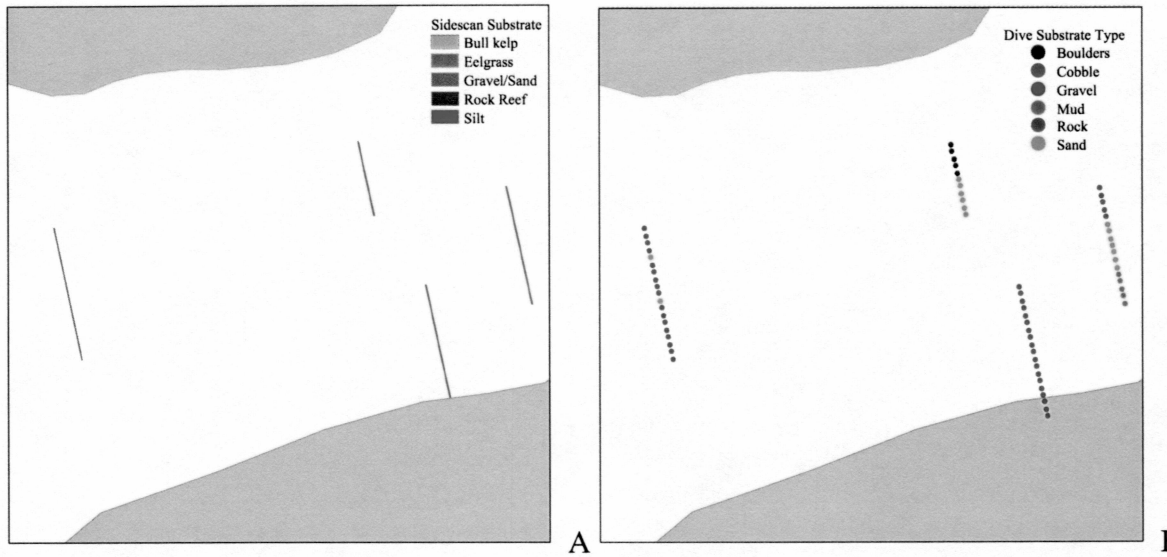


Figure 5. Example of overlapping sidescan sonar (Holland-Bartels et al. 1998) and ADF&G dive survey (Becker and Biggs 1992) transects. The sidescan sonar classifications are shown in Box A. Box B shows the dive survey substrate classifications that overlap the sidescan sonar transects in Box A.

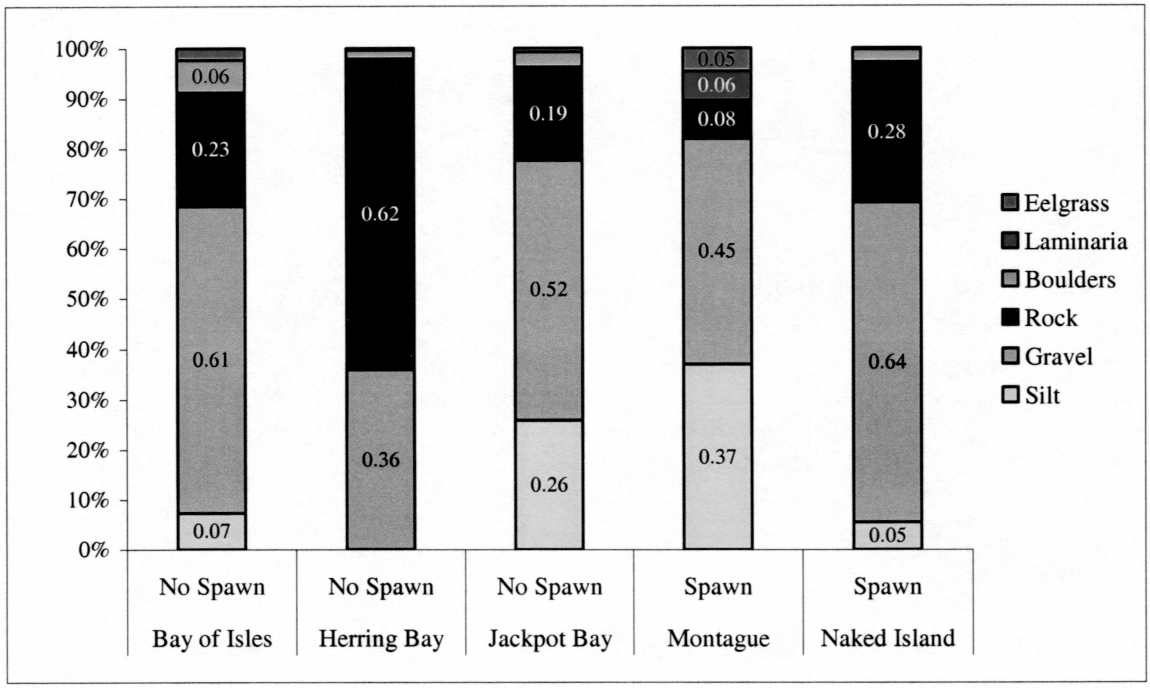


Figure 6. Proportion of each bottom type in the areas surveyed with sidescan sonar during the Nearshore Vertebrate Predator study in Prince William Sound (Holland-Bartels et al. 1998).

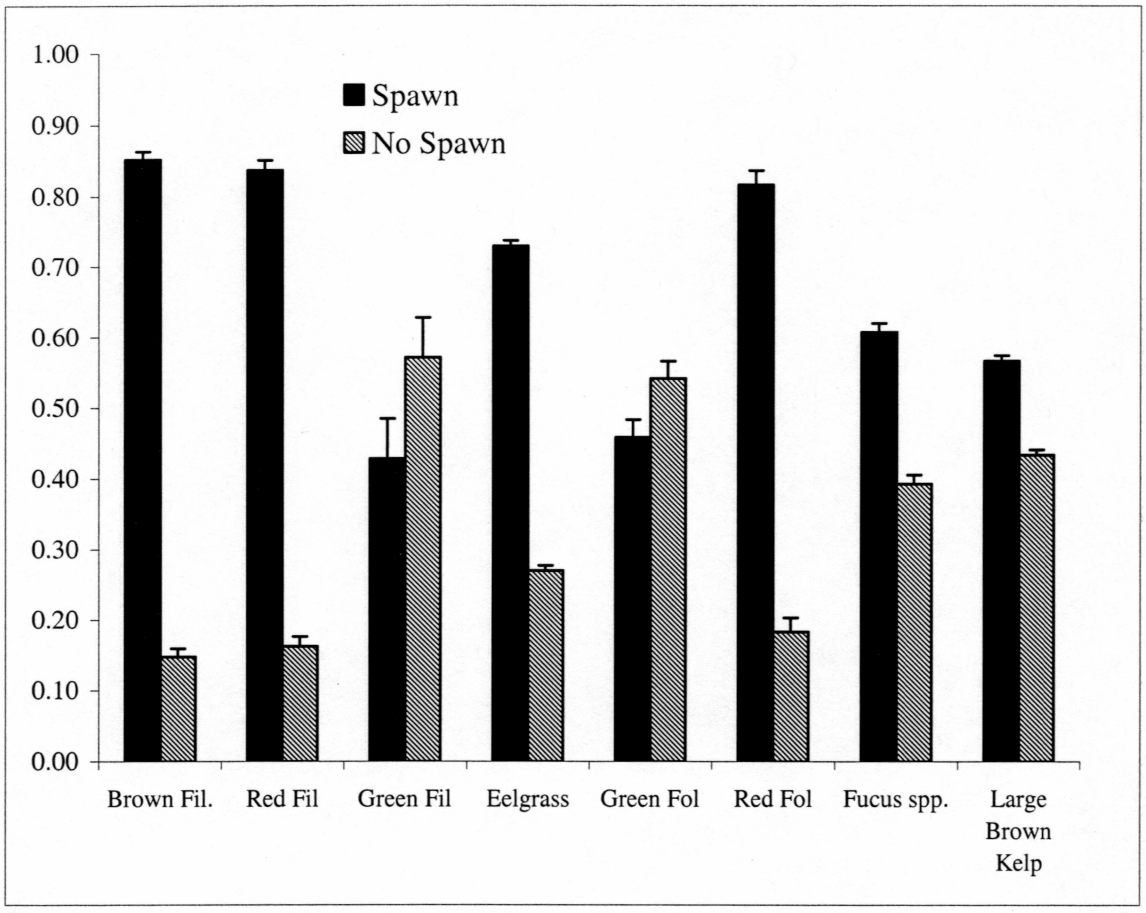


Figure 7. Proportion of occurrences of herring spawn present and absent on each vegetation type in the ADF&G dive survey database. Error bars represent the standard errors of the proportions.

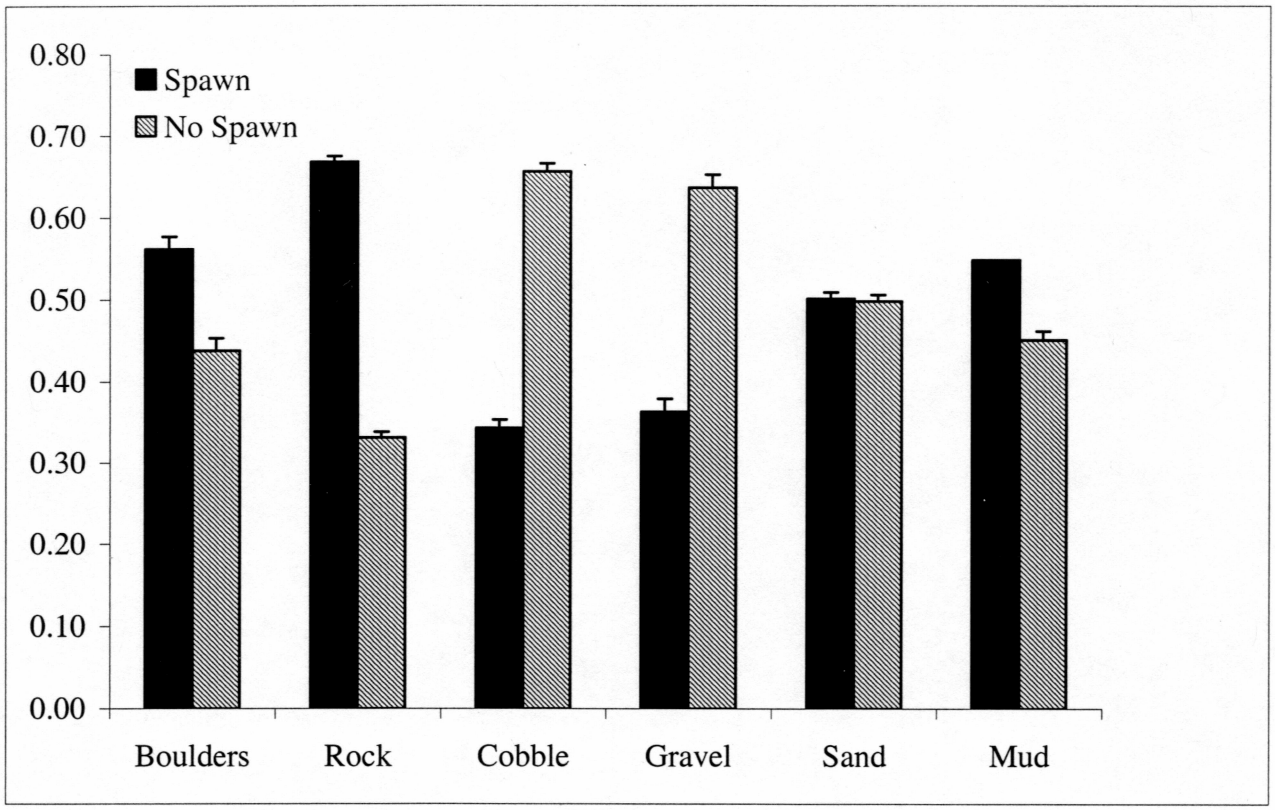


Figure 8. Proportion of occurrences of herring spawn present and absent on each substrate type in the ADF%G dive survey database. Error bars represent the standard errors of the proportions.

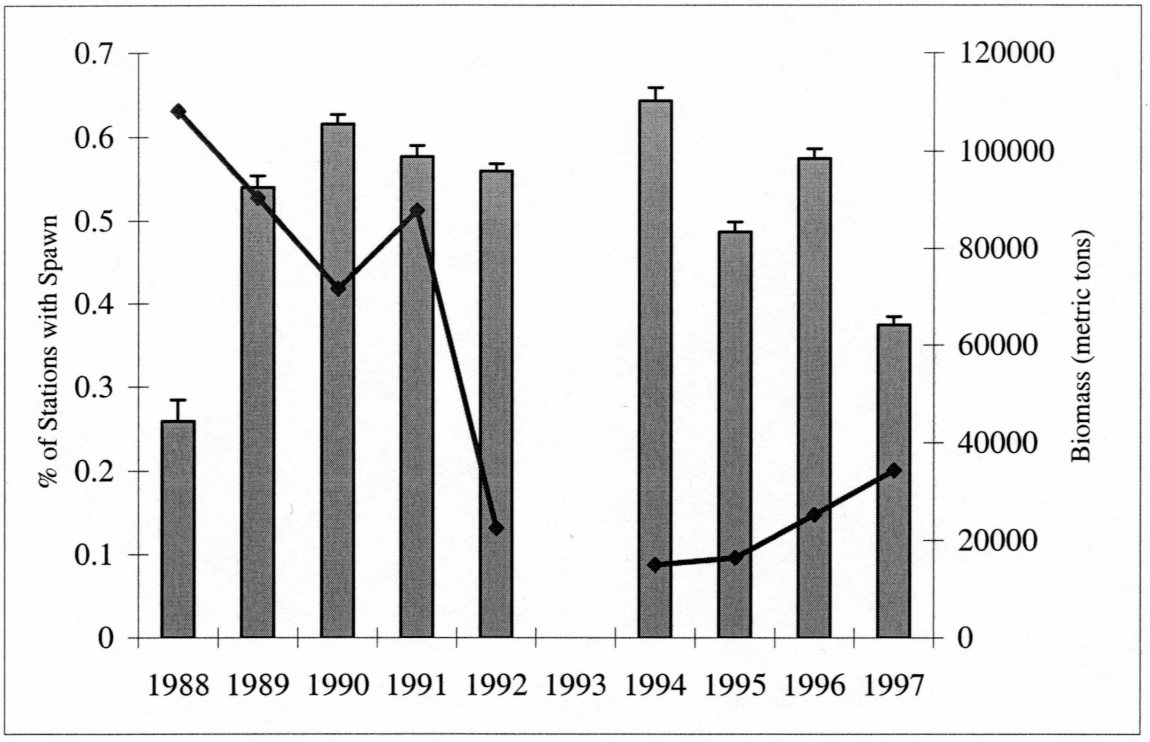
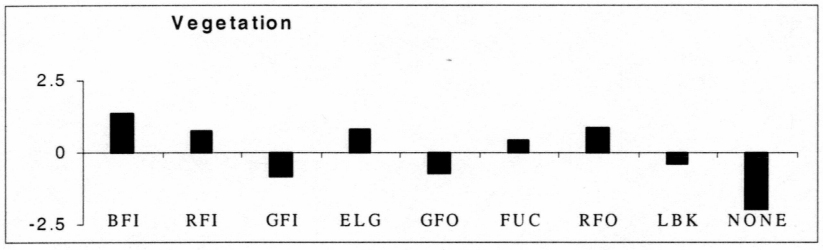
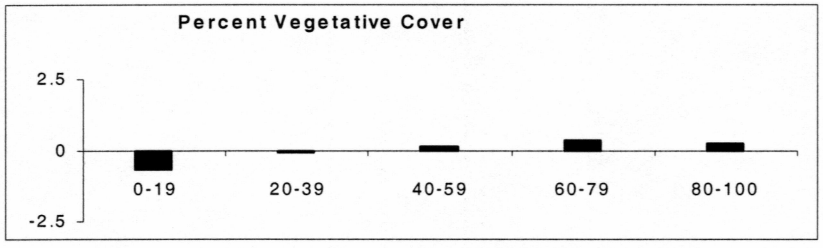
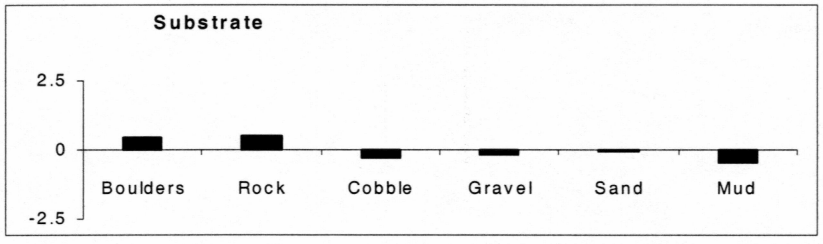
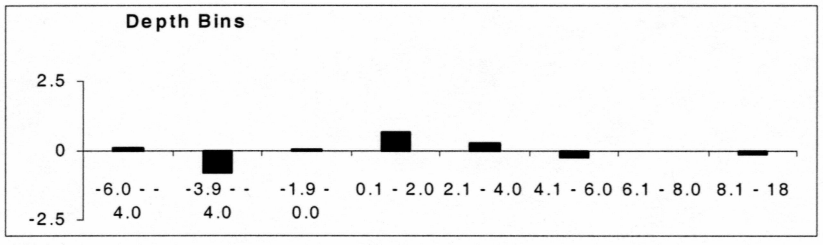


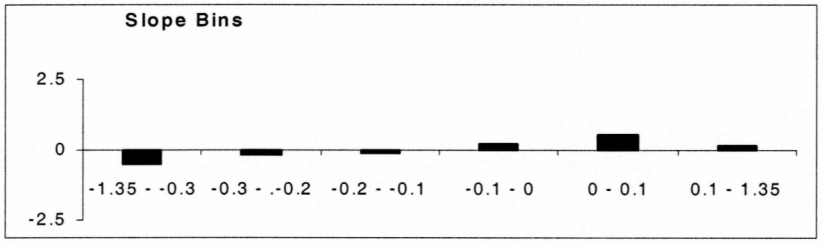
Figure 9. Percent of ADF&G dive survey stations containing herring spawn each year (bars) and annual PWS herring biomass in metric tons (black line)(Sharp et al. 2000). The percent of stations containing spawn was not significantly correlated with spawning stock biomass (r^2 = 0.13).


Vegetation
2.5
0
-2.5
BFI
RFI
GFI
ELG
GFO
FUC
RFO
LBK
NONE


Percent Vegetative Cover
2.5
0
-2.5
0-19
20-39
40-59
60-79
80-100


Substrate
2.5
0
-2.5
Boulders
Rock
Cobble
Gravel
Sand
Mud


Depth Bins
2.5
0
-2.5
-6.0 - - 4.0
-3.9 - - 4.0
-1.9 - 0.0
0.1 - 2.0
2.1 - 4.0
4.1 - 6.0
6.1 - 8.0
8.1 - 18


Slope Bins
2.5
0
-2.5
-1.35 - -0.3
-0.3 - .-0.2
-0.2 - -0.1
-0.1 - 0
0 - 0.1
0.1 - 1.35

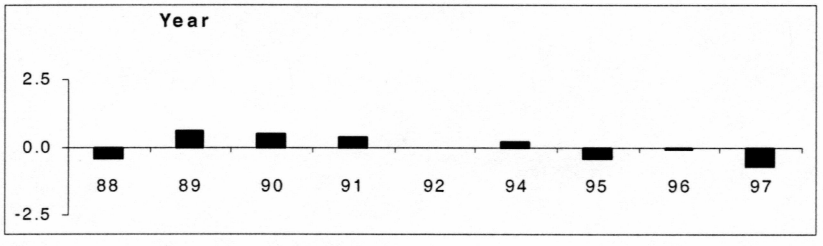

Year
2.5
0.0
-2.5
88
89
90
91
92
94
95
96
97

Figure 10. Coefficients of the linear predictors from the reduced, main-effects generalized linear model for predicting the probability of herring spawn given the following predictor variables: vegetation type (BFI = brown filamentous algae, ELG = eelgrass, FUC = *Fucus* sp., GFI = green filamentous algae, GFO = green foliose algae, LBK = large brown kelp, RFI = red filamentous algae, RFO = red foliose algae, and NONE = no vegetation), percent cover (percent vegetative cover), substrate type, depth (m), slope (negative slopes indicate a downward sloping station), and year. The coefficients show the strength and direction of the relationship between each category of the predictor variables and the probability of the presence of spawn.

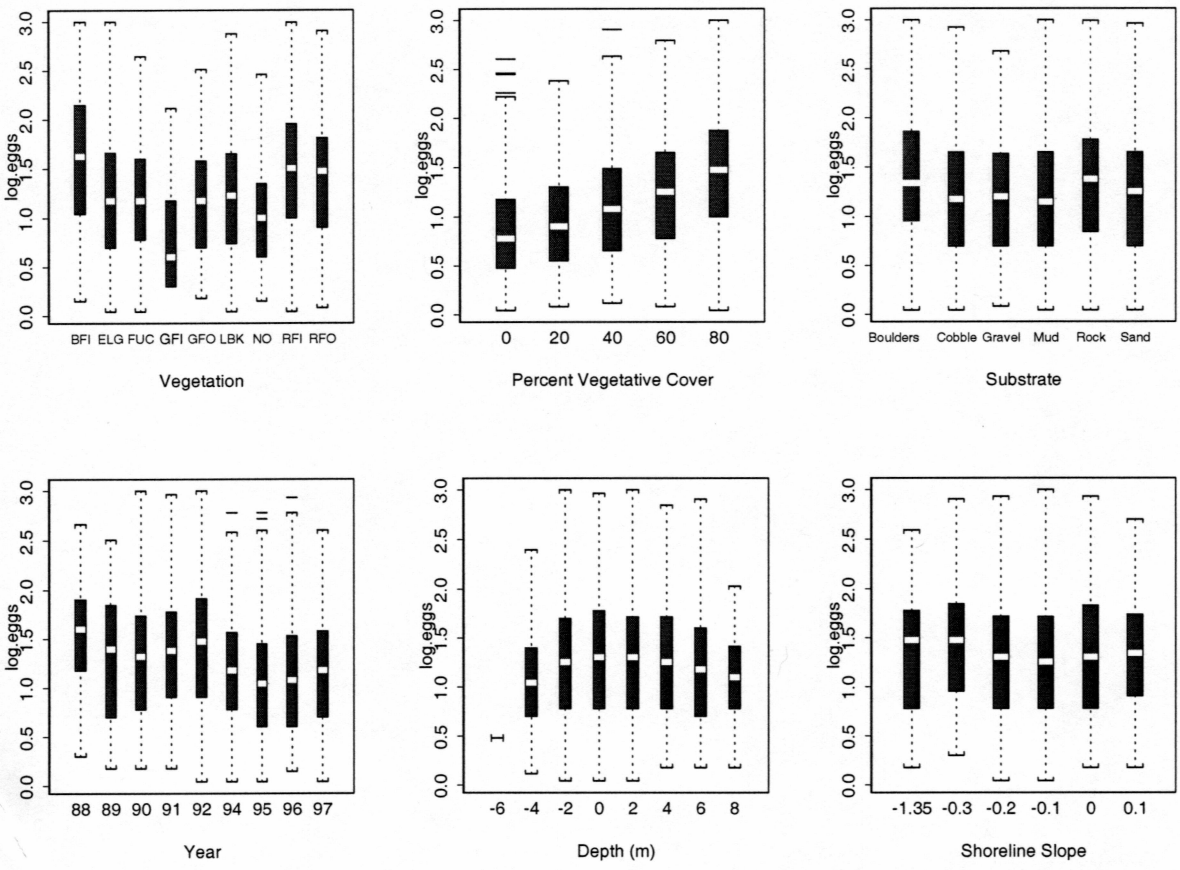


Figure 11. Boxplots showing the distribution of the $\log_{10}$ transformed herring egg densities from the ADF&G dive surveys for each category of the independent variables contained in the full multi-way ANOVA. (Vegetation types: BFI = brown filamentous algae, ELG = eelgrass, FUC = *Fucus* sp., GFI = green filamentous algae, GFO = green foliose algae, LBK = large brown kelp, RFI = red filamentous algae, RFO = red foliose algae, and NO = no vegetation).

Table 1. Mean, standard error, maximum and minimum values, and upper and lower 95% confidence intervals for depth (m), percent vegetative cover, and slope for herring spawn and no spawn stations in the ADF&G dive survey database.

	Depth		Percent Cover		Slope	
	No Spawn	Spawn	No Spawn	Spawn	No Spawn	Spawn
Mean	1.758	1.712	26.860	57.300	-0.070	-0.053
SE	0.039	0.024	0.410	0.420	0.001	0.001
Max	16.16	15.24	100.00	100.00	0.79	1.34
Min	-4.573	-4.268	0.000	0.000	-1.220	-1.037
Lower 95% CI	-1.691	1.665	26.060	56.500	-0.072	-0.055
Upper 95% CI	1.824	1.760	27.700	58.100	-0.068	-0.051

Table 2. Results from the full main-effects GLM for determining the probability of herring spawn given vegetation type, percent vegetative cover, depth, substrate type, slope, and year. This table shows the amount of deviance explained and p-values (chi-square) by factor and the total deviance explained by the full main-effects GLM fit with herring spawn presence/absence data from the ADF&G dive survey database.

		Deviance Explained		
Factor	DF	Deviance	%	P value
Vegetation	8	4984.49	23.70%	<0.001
Percent Vegetative Cover	4	338.33	1.61%	<0.001
Depth	7	225.24	1.07%	<0.001
Substrate	5	411.63	1.96%	<0.001
Slope	5	95.21	0.45%	<0.001
Year	8	380.10	1.81%	<0.001
Geography	1	0.10	0.00%	0.78
Null Deviance				21031.58
Residual Deviance				14596.48
Percent Deviance Explained				30.60%

Table 3. Results from the GLM for determining the probability of herring spawn given vegetation type, percent vegetative cover, depth, substrate type, slope, year, and interaction effects for vegetation and substrate, and vegetation and depth. This table shows the amount of deviance explained and p-values (chi-square) by factor and the total deviance explained by the GLM fit with herring spawn presence/absence data from the ADF&G dive survey database.

		Deviance Explained		
Factor	DF	Deviance	%	P value
Vegetation	8	4984.49	23.70%	<.001
Percent Vegetative Cover	4	338.33	1.61%	<.001
Depth	7	225.24	1.07%	<.001
Substrate	5	411.63	1.96%	<.001
Slope	5	95.21	0.45%	<.001
Year	8	380.10	1.81%	<.001
Vegetation * Substrate	40	395.49	1.88%	<.001
Vegetation *Depth	38	138.10	0.66%	<.001
Null		21031.58		
Residual		14062.99		
Percent Deviance Explained		33.13%		

Table 4. Results from the multi-way ANOVA of herring egg density given the following predictor variables (vegetation type, percent vegetative cover, substrate type, depth, slope, and year) and interaction terms for vegetation and substrate, and vegetation and depth.

Term	DF	SS	Mean Sq	F Statistic	P-Value
Vegetation	8	129.22	16.15	57.22	< 0.001
Substrate	5	31.85	6.37	22.56	< 0.001
Depth	7	6.96	0.99	3.52	0.001
Percent Vegetative Cover	4	281.34	70.34	249.15	< 0.001
Slope	5	5.35	1.07	3.79	0.002
Year	8	131.01	16.38	58.01	< 0.001
Vegetation x Substrate	35	90.44	2.58	9.15	< 0.001
Vegetation x Depth	32	17.06	0.53	1.89	0.002
Residuals	6387	1803.08	0.28		

Table 5. Results from the multi-way ANOVA of herring egg density given the following predictor variables (vegetation type, percent vegetative cover, substrate type, depth, slope, and year) and an interaction term for vegetation and substrate.

Term	DF	SS	Mean Sq	F Statistic	P-Value
Percent Vegetative Cover	4	310.92	77.73	273.44	<0.001
Year	8	135.99	17.00	59.80	<0.001
Vegetation	8	107.54	13.44	47.29	<0.001
Substrate	5	23.70	4.74	16.67	<0.001
Vegetation x Substrate	35	90.00	2.57	9.05	<0.001
Residuals	6431	1828.16	0.28		

Appendix A

Seaweeds from the dive survey database and their corresponding grouping

Group	Code	Phylum	Common Name
Brown Filamentous Algae	BFI	Phaeophyta	Brown hair kelp
			Wheat straw kelp
			Desmarestia
			Miscellaneous Hair Kelp
			Brown filamentous
			Hot dog kelp
			Brillo pad kelp
Eelgrass	ELG	Zostera	Eelgrass
Fucus	FUC	Phaeophyta	Cut fucus
			Rockweed
Green Filamentous Algae	GFI	Chlorophyta	Green filamentous
			Chlorophyta
			Sea lettuce

Group	Code	Phylum	Common Name
Large Brown Kelp	LBK	Phaeophyta	Agarum
			Alaria
			Brown bulb
			Costaria
			Elephant ear
			Ribbon / sugar wrack
			Laminaria
			Bull Kelp
			Seer Sucker Kelp
Red Filamentous Algae	RFI	Rhodophyta	Red hair
			Coraline
			Red grass
			Red fireweed
			Red fern or firweed
			Red fern
			Corkscrew
			Red filamentous
Red Foliose Algae	RFO	Rhodophyta	Red leaf, fucus-like
			Red cup
			Tube kelp
			Red blade
			Dulce, red leaf
			Red leaf, irridescent

Appendix B

Count and frequency of each vegetation type from the dive survey database used in the fine-scale presence/absence analysis and egg density analyses

	Presence/Absence		Egg Density	
Vegetation Type	Count	Frequency of Occurrence	Count	Frequency of Occurrence
Brown Filamentous Algae	967	6%	699	11%
Red Filamentous Algae	695	5%	542	8%
Green Filamentous Algae	77	1%	19	0%
Eelgrass	3,394	22%	1,902	29%
Green Foliose Algae	410	3%	122	2%
Red Foliose Algae	382	3%	262	4%
Fucus sp.	1,493	10%	726	11%
Large Brown Kelp	4,441	29%	2,088	32%
No Vegetation	3,349	22%	132	2%
Total	15,208		6,492	